OBSERVATIONS OF THE FEEDING MECHANISM OF A CTENOPHORE, *MNEMIOPSIS LEIDYI*.[1]

ROLLAND J. MAIN.

Observations of the feeding habits of ctenophores are scattered through the literature dealing with these organisms (Bigelow, '15; Lebour, '22–'23; Mayer, '12; Nelson, '25), but as yet no detailed study of the feeding mechanism has appeared.

The ciliation of a hydromedusa has been studied (J. F. Gemmill, '19), but this compares in no way with the complex food catching apparatus of a ctenophore such as *Mnemiopsis leidyi*. The morphological work done upon this ctenophore is incomplete, for neither Agassiz (1849), Fewkes (1881), nor Mayer ('12), mention the presence of its remarkable mechanism for the capture of food.

Mnemiopsis leidyi through its habit of devouring the free-swimming larvæ of the oyster and of other molluscs becomes of such economic importance that it is of interest to determine by what means these organisms are captured and carried into the stomodæum, and how the undigested residues are discharged.[2]

Materials and Methods.

The specimens of *Mnemiopsis leidyi* were obtained in the northern half of Barnegat Bay, N. J., a shallow estuary, in water of a specific gravity approximating 1.010, with temperatures close to 20° C., during August and the first part of September, 1926. The animals were caught in a net, placed in jars without injury and within ten minutes after capture they were being examined under the binocular.

Living plankton was used to determine the feeding mechanism, and it is felt that to this the success of the experiment is pri-

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marily due, since it is doubtful for reasons given below whether any other material could have been successfully used. The plankton was secured by pouring sea water through a 200 mesh plankton net, and concentrating the organisms in a small amount of water. A *Mnemiopsis* was placed in a watch crystal under the binocular, a little of the plankton culture was added, and the reactions of the ctenophore noted.

Structure and Operation of the Food Catching Mechanism.

To understand the mechanism of the food catching apparatus, it is first necessary to have a clear idea of the gross anatomy of *Mnemiopsis*, Fig. 1. Although considerable work has been done

Fig. 1. Adult *Mnemiopsis leidyi* from Barnegat Bay. Photographed immediately after fixation in 10 per cent. hydrochloric acid. The oral lobes have contracted to approximately 2/3 the length characteristic of the living animal. Photographed by T. C. Nelson.

on the morphology of the animal, all the writers have apparently disregarded the presence of a definite ridge, an extension of the lips of the mouth, which the writer has named the "labial ridge." [3]

There are four furrows formed by the juncture of the oral lobes with the body. In each furrow along the inner side of the labial ridge is a line of tentacles. Through the base of this labial ridge runs a branch of the paragastric canal, which finally unites with the auricular canal. On the opposite side of this ridge is the ciliated channel for conveying food to the mouth, Figs. 2 and 3.

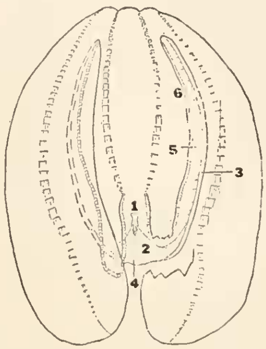

FIG. 2. *Adult Mnemiopsis leidyi.* Part of the right lobe and the tip of the right auricle have been omitted. It is difficult to represent the turning of the labial ridge. The lips are in the plane of the paper. As the lip becomes the labial ridge, it turns so that it lies in a plane at right angles to the paper. 1. The tentacular bulb. 2. The tentacular ridge, with tentacles. 3. The labial ridge, along which runs the tentacular ridge. 4. Lip. 5. Auricular groove. 6. Cilia of auricle.

To this channel, or trough, will be applied the term "labial trough." It is formed by the labial ridge on one side, and the oral lobe on the other. It runs along the ridge to the point where the ridge becomes the lip, and here the trough runs directly into the corner of the mouth, Fig. 4. The labial ridge is separated from the cilia of the auricles by the auricular groove in which the cilia of the auricle beat, and at the bottom of which lie the tentacles stretched out in the current.

[3] The writer calls attention to some apparent discrepancies in earlier work on *Mnemiopsis leidyi.* Fewkes pictures an adult of this species which differs widely from the type obtained from Barnegat Bay. The latter, save for the contraction of the oral lobes, is well illustrated in Figure I. Fewkes' figure shows the surface of the animal covered with discoidal warts which are claimed by Mayer to be present in *M. mccradyi* and in *M. gardeni* but absent in *M. leidyi.* Fewkes' figure differs also in the shape of the body.

Near the mouth the line of tentacles curves away from the labial ridge up to the tentacular bulb. The tentacles are placed irregularly along this line, usually in groups, some animals having

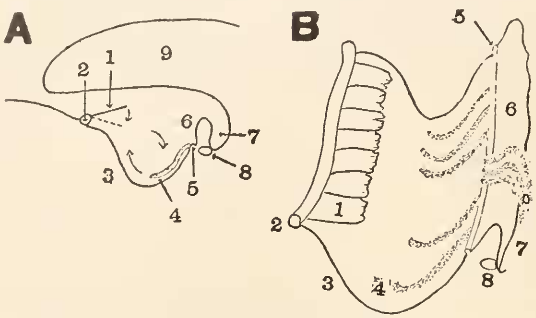

FIG. 3. *A*. Cross section of auricular groove. The cilia of the auricle (1) beat up and down as indicated by the arrow and dotted line. The other two arrows show the direction of the current produced by the cilia. 1. Cilia of auricle. 2. Auricular canal. 3. Auricular groove. 4. Tentacle. 5. Tentacular ridge. 6. Labial ridge. 7. Labial trough. 8. Branch of paragastric canal. 9. Oral lobe. *B*. View of auricular groove from above. The oral lobe has been laid back. Parts correspond to Fig. 3*A*. Three tentacles are here shown putting food in the labial trough, where it will be drawn off and conveyed to the mouth.

many more tentacles than others. This may be due to the fact that they have been broken off in securing food, for often food may be seen entering the stomodæum with portions of tentacles attached.

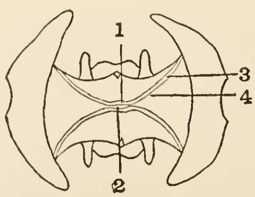

FIG. 4. Oral view of adult *Mnemiopsis leidyi*. This shows how the lips are continued into the labial ridge and how the trough runs into the mouth. 1. Lip. 2. Mouth. 3. Labial ridge. 4. Labial trough.

When a particle of food is caught in the current produced by the cilia in the grooves it is whirled about until it finally touches a tentacle. This entangles it, often with the aid of several other tentacles. These tentacles then contract, and apparently are drawn over the labial ridge into the labial trough, presumably by cilia, Fig. 3*B*. Here they stretch out in the direction of the mouth, the food is drawn off, and passes down toward the mouth. The tentacles then relax, and resume their normal position. Often several pieces of food are beaten about for some time in the groove. Dirt in the groove is gradually entangled in mucus into a long thread which slowly passes out at the aboral end of the groove. If much dirt be present, the whole animal pulsates, contracting the groove and forcing out all material present. The tentacles were never seen placing any foreign material into the labial trough, unless a little happened to be caught up with the food. Possibly it is for these reasons that *Mnemiopsis leidyi* is not found in muddy waters, since it will not seize food if much dirt be present. Carmine introduced directly into the labial trough is drawn along but for a short distance, and then is passed out over the labial ridge. For this reason the use of the natural plankton food organisms in studying the mechanism is imperative.

It is here that we must search for the explanation of why *Mnemiopsis leidyi* lives so largely upon bivalve larvæ, in spite of the great preponderance of other plankton in the water (Nelson, '25). The writer has observed that often the ctenophore is unable to hold an active copepod. Possibly the stronger swimmers are able to escape the ciliary currents, whereas the young oyster shuts its shell on contact and is therefore an easy prey. Polychæte larvæ were found in *Mnemiopsis* at this time, although never more than one or two per animal. This is contrary to Nelson's ('25) belief that it would be almost impossible for this ctenophore to ingest such a prey.

Food captured by the tentacles about the mouth was passed down directly over the lips into the mouth, often aided by a contraction of the lips, bringing them near the tentacular bulb. After the food has passed into the stomodæum, it usually proceeds slowly to the center, between the two paragastric canals, close to the convoluted tubules which probably secrete the digestive juices. It may, however, lodge below this point, Fig. 5. Sometimes it is caught in the swifter current at the very edge of the stomodæum, and is whirled up to the beating cilia at the aboral end. Here it is usually turned back, for these cilia seem to act partly as filters. At times, however, a particle may be squeezed through and enter the funnel to pass around in the food canals.

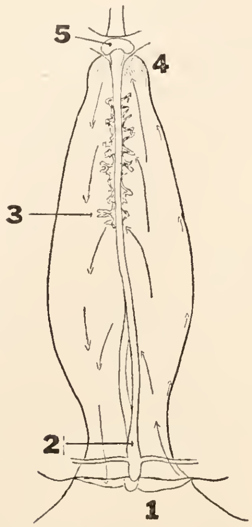

FIG. 5. The stomodæum of *Mnemiopsis leidyi*. In order to avoid confusion, the paths taken by ingested food are shown on the right side only. The larger arrows are the more usual paths. The smaller arrows on the extreme right denote a swifter current, in which the food sometimes travels. On the left half only, are shown the paths taken by the excreted materials. 1. Mouth. 2. Paragastric canal. 3. Digestive glands? 4. Cilia. 5. Funnel.

The undigested material in the stomodæum is passed down as indicated, and ejected through the mouth. These paths are not definite, for incoming food will pass a certain spot, and immediately afterwards outgoing wastes will cross the same spot going in the opposite direction. Those particles which have passed through into the food canals may reënter the stomodæum and pass out through the mouth, or they may follow the usual procedure for material in the canals, and be voided at the anus.

Just before defecation occurs, particles may be seen gathering about in the funnel and in the axial funnel canal. Then one of the branches of this canal elongates above the surface and the particles are forced out through the pore. The current in all the food canals now seems to be in the direction of the funnel. By this time the cilia of the aboral end of the stomodæum have ceased beating, and the whole upper end of the stomodæum presents a contracted appearance, Fig. 6. After the particles of waste have

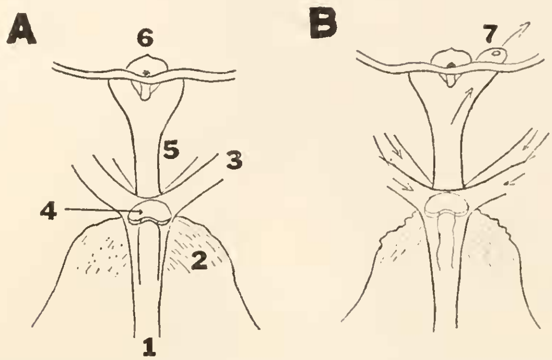

Fig. 6. Aboral portion of stomodæum, and axial funnel canal of *Mnemiopsis leidyi*. *A*. Before defecation. 1. Paragastric canal. 2. Cilia. 3. Food canals. 4. Funnel. 5. Axial funnel canal. 6. Sense organ. 7. Excretory pore. *B*. During defecation, arrows showing direction of waste. Note shrunken appearance of stomodæum.

all passed out the cilia begin beating again, and the branch of the funnel canal slowly retracts. Although several successive defecations of specimens have been observed, only one branch was used, and in no specimen was the use of both branches observed.

The Early Development of the Food Catching Mechanism.

Since the complex food catching apparatus is present only in the adult *Mnemiopsis,* the question of its ontogeny naturally arises. The young were plentiful at the time of this study, and various stages were examined.

The smallest specimens obtained were in the Cydippidæ-stage, approximately 2 mm. high and 2 mm. broad, Fig. 7. These possess two long branching tentacles with no trace of the tentacular ridge, labial ridge, or labial trough. They feed by capturing the food with the tentacles, retracting them, and drawing them down over the lip and into the stomodæum, where the food is drawn off. Another contraction, and the tentacles emerge, to again float up above the animal.

The next step in development was found in a 6 mm. specimen, Fig. 8. This stage has still the two compound tentacles.

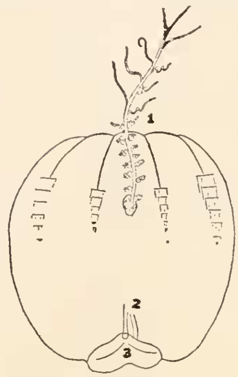

FIG. 7. Young *Mnemiopsis leidyi,* 2 mm. high. 1. Branching tentacle, partially contracted. 2. Paragastric canals, only unbranched terminations shown. 3. Mouth.

The 8 mm. specimens are much further advanced, Fig. 9. The auricles are now forming, and the tentacular ridge has appeared as a slight fold or line as shown, but it is not connected to the tentacular bulb, and possesses no tentacles. It was observed that tentacles never appeared along the tentacular ridge until it had joined the tentacular bulb.

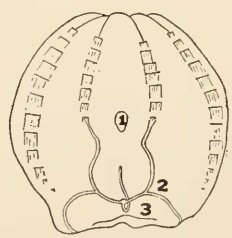

FIG. 8. Young *Mnemiopsis leidyi,* 6 mm. high. 1. Tentacular bulb. (Tentacle omitted, being same as in Fig. 7.) 2. Juncture of paragastric and auricular canals. 3. Mouth.

It is now easy to see how the adult structures are completed. As the junction of the paragastric and auricular canals moves upward forming the auricular groove, the tentacular ridge and labial ridge grow with it. The large branched tentacle disappears, and small tentacles appear along the tentacular ridge.

This remarkable food catching apparatus of *Mnemiopsis,* in which the conveying system seems to foreshadow that of the bivalves, is certainly a great advance over that of the Scyphozoa.

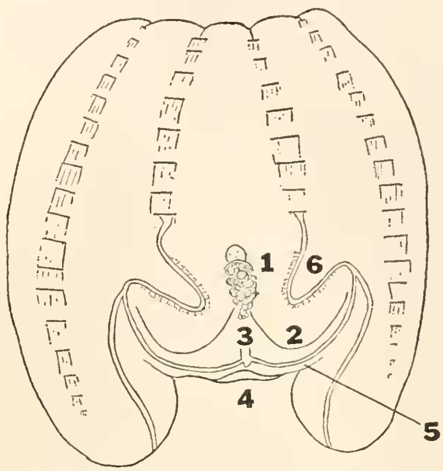

FIG. 9. Young *Mnemiopsis leidyi,* 8 mm. high. 1. Branched tentacle entirely retracted, but same as in Fig. 7. 2. Tentacular ridge. 3. Paragastric canal, termination shown with branches. 4. Mouth. 5. Beginning of labial ridge. 6. Developing auricles.

Of its efficiency there can be no doubt, for compare Bigelow's ('15) statement that the plankton was greatly diminished in a swarm of ctenophores. Nelson ('25) also brings forth evidence of a correlation between the abundance of *Mnemiopsis leidyi* and the intensity of shipworm infestation and oyster sets. Moreover, the fact that the ctenophores are usually found in such vast and dense swarms, argues well for their ability to obtain food. Possibly it is due to this efficient apparatus that we find in many species of ctenophores the small compact bodies and absence of long trailing tentacles.

SUMMARY.

The mode of feeding was studied in young tentacled forms and in the adult *Mnemiopsis leidyi.* The young capture food with their branched tentacles, and deposit it in the mouth. The adults entangle the food with the small tentacles along the tentacular ridge, and deposit it in the labial trough, whence it is carried to the mouth.

Food enters the stomodæum and after digestion is cast out of the mouth, or it may enter the food canals and pass out of the anus.

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